19. INTERACTIONS BETWEEN SOIL ARTHROPODS AND MICROORGANISMS IN CARBON, NITROGEN AND MINERAL ELEMENT FLUXES FROM DECOMPOSING LEAF LITTER

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SUMMARY

The release of nitrogen (and other limiting nutrients) from litter for root uptake primarily depends upon the balance between mineralization and immobilization processes. Soil animals do not appear to contribute to these processes directly in temperate forest soils but have important local effects on net mineralization rates through interactions with fungal and bacterial populations. These effects vary qualitatively and quantitatively between major groups of soil animals.

Macroarthropods (e.g. woodlice and millipedes) can enhance microbial respiration but feeding intensities above optimal values decrease microbial activity and result in gross shifts in the balance of fungal and bacterial populations. This effect appears to be related to the sensitivity of the fungal thallus to disruption and the favourable environment of saprotroph guts for bacterial growth.

Microarthropods such as collembola feed selectively on fungi and the inhibitory effects of grazing may be more marked than those of litter-feeding animals. However, the effects of fungal food quality on collembola populations, and the relationships between litter microhabitat complexity and the availability of hyphae, have important modifying influences on grazing effects.

Leaching rates of cations (calcium, potassium and sodium) from leaf litter are enhanced by soil animal feeding activities but the effects are proportionally much smaller than the impact of animals on nitrogen mineralization as ammonium. Woodlice (*Oniscus*) and millipedes (*Glomeris*) enhanced ammonium leaching rates up to six times control values without animals. The response was proportional to the number of *Oniscus* but increasing numbers

of *Glomeris* above optimum values reduced ammonium leaching rates. These effects are not directly related to nitrogen excretion by the animals and qualitative influences of the animals on the litter microflora are implicated.

It is concluded that soil animal feeding activities can significantly affect nitrogen mineralization rates through locally reducing fungal immobilization. Some nitrogen from food materials may be transferred to bacterial biomass during gut passage but continued growth in faecal material is limited by available carbon and energy resources so that excess nitrogen can be taken up by roots and mycorrhizas as ammonium. Protozoa and nematodes may be involved in nitrogen release from the residual bacterial biomass.

INTRODUCTION

The importance of animal microbial interactions in decomposition and nutrient cycling processes has been demonstrated for aquatic systems both in the field (Cooper 1973, Flint & Goldman 1975; Nixon, Oviatt & Hale 1976) and laboratory (Barsdate, Fenchel & Prentki 1974; Fenchel & Harrison 1976; McDiffett & Jordan 1978) but little is known about equivalent processes in soils.

Microbial biomass and respiration exceed that of the soil fauna by one or two orders of magnitude and it is frequently assumed, with the exception of termites (Wood & Sands 1977) and burrowing earthworms, that the fauna has little significance in soil processes. Over recent years, however, there has been increasing appreciation that the observed levels of microbial activity are the sum effects of phenomena operating in a mosaic of microsites in litter, soil and the rhizosphere which are highly variable in time and space. At this scale of organization the fauna can be seen to affect soil processes indirectly through the formation of microsites (litter comminution, burrowing activities and faecal aggregates) as well as through direct effects of feeding on fungal and bacterial populations.

Earthworms in temperate, agricultural soils have been shown to qualitatively and quantitatively modify the microflora (Parle 1963), affect patterns of root growth (Aldag & Graff 1974; Edwards & Lofty 1978), increase the availability of nitrogen, phosphorus and mineral nutrients (Graff 1970; Syers, Sharpley & Keeney 1979) and influence transport pathways of dissolved nutrients (Sharpley, Syers & Springett 1979). A large earthworm biomass is not, however, characteristic of most soil types and the effects of other temperate invertebrate groups on soil processes are difficult to quantify under field conditions.

Patten & Witkamp (1967) used laboratory microcosms containing tree seedlings, litter, soil, millipedes and microbial components to demonstrate

that the animals were integral to the transfers of ^{137}Cesium from litter back to the plants. Similar results were obtained by Witkamp & Frank (1969, 1970) for transfers of ^{137}Cesium as well as potassium and magnesium. The addition of millipedes or snails to decomposing leaf litter reduced microbial ^{137}Cesium immobilization from 36.0 to 10.8% of the initial litter content through the consumption of the litter microflora (Witkamp & Frank 1969). This process was considered critical by Ausmus, Edwards & Witkamp (1976) for the turnover of nutrients in a warm temperate, deciduous forest. The immobilization of nitrogen, phosphorus and potassium in microbial biomass was highest in summer and autumn (fall) and lowest in spring during the period of maximum root growth. The nutrient transfers to the smaller faunal biomass were highest during this period but excess nutrients to saprotroph demands were not lost to ground water because of active root uptake. The soil fauna was predominantly mycophagous and was calculated to consume 86% of fungal production in this site (McBrayer 1974). During periods of high rainfall and low root growth the immobilization of limiting nutrients in the soil biota (including mycorrhizas) was considered to be a major process preventing leaching from the rooting zone of the soil profile. Similar processes have been quantified for simulated rhizosphere systems in which bacterially immobilized phosphorus was mobilized through the feeding activities of amoebae (Cole *et al.* 1978).

Thus there is evidence that soil faunas affect nutrient fluxes in soils through their influence on microbial mineralization and immobilization. We therefore briefly review these basic processes before considering the mechanisms involved in the direct and indirect effects of soil animals on nutrient flux rates and pathways.

MINERALIZATION AND IMMOBILIZATION

The twin processes of mineralization and immobilization are invariably involved in decomposition since catabolism provides the energy and nutrients required for the maintenance, growth and reproduction of saprotrophic organisms (Swift, Heal & Anderson 1979). The balance of these processes (net mineralization) determines the nutrient supply to higher plants and relates directly to the availability of that element to the organisms (fungi, bacteria and animals) involved in organic matter decomposition.

Sodium and potassium are usually available in excess of saprotroph requirements. These elements are predominantly present as inorganic ions and are leached rapidly from decaying litter. The loss rates generally decrease with time as concentrations in the litter approach those for microbial tissues (Gosz, Likens & Bormann 1973).

Under laboratory conditions microbial immobilization of potassium may be up to 80% higher than the retention in leached, sterile-litter controls (Witkamp & Barzansky 1968). This suggests that the ion exchange complex of litter (as opposed to humus) is less efficient than microorganisms for the retention of these mobile cations.

All nitrogen and sulphur, some calcium and most phosphorus, are present in organic compounds in plant and animal remains and are mobilized through enzyme activity. The availability of nitrogen and phosphorus limits secondary production in the soil, just as they limit primary production in most natural terrestrial ecosystems, and these elements are therefore efficiently annexed and conserved by microorganisms.

During the course of decomposition the carbon/nitrogen ratio decreases (as well as ratios for other limiting nutrients), and microbial tissues represent an increasing proportion of the resource mass. Swift (1973) found that sawdust lost 39% of the initial weight after 15 weeks' incubation in the laboratory but 39% of the remaining material was fungal mycelium. Nitrogen is not theoretically mobilized until the carbon/nitrogen ratio of the resource complex approaches that of microbial tissues (about 10/20:1, depending upon species and growth conditions); similar principles underlie the release of other microbially bound nutrients. In acid, organic soils, such as moorlands, tundra, coniferous forests and mor-humus forms in deciduous forests, the carbon/nitrogen ratio of soil organic matter may be considerably above the threshold value where nitrogen mineralization theoretically occurs.

A critical step in nutrient cycling processes is therefore the release of nutrients from microbial tissues. This involves abiotic processes such as freezing/thawing and wetting/drying cycles which occur in soils subject to variable extremes of weather and climate (Witkamp 1969; Witkamp & Frank 1970) but biotic processes are probably more important under temperate conditions. Microbial lysis and autolysis undoubtedly contribute to the turnover of bacterial and fungal tissues (Mitchell & Alexander 1963; Shields *et al.* 1973) but the result of microcosm experiments suggests that soil fauna feeding activities are quantitatively more important. The feeding activities of soil fauna are also widely stated to stimulate microbial growth and activity through the grazing of senescent tissues. The balance of bacterial and/or fungal growth and fauna consumption is therefore an important variable in determining net mineralization rates.

The soil fauna may therefore affect the availability of inorganic nitrogen in three ways: by the enhancement of carbon mineralization and hence the reduction of litter carbon/nitrogen ratios, by the stimulation or reduction of microbial biomass and the excretion of nitrogen compounds. The evidence for

these phenomena is reviewed before considering their possible contribution to nitrogen fluxes in the soil.

Effects of soil animals on microbial respiration

Van der Drift & Witkamp (1960) and Nicholson, Bocock & Heal (1966) suggested from a comparison of microbial respiration rates on arthropod faeces, mechanically ground litter and intact leaves that the main contribution of soil animals to decomposition processes was the short-term enhancement of microbial activity through litter comminution. A criticism of these experiments is that they involved the 'static' effects of a single gut passage rather than the continuous 'dynamic' effects of coprophagy and direct grazing on microbial populations. Thus Nicholson, Bocock & Heal (1966) found no significant differences in weight losses after one year in the field between millipede faeces and intact leaves enclosed in fine-mesh litter bags. Standen (1978), however, demonstrated that enchytraeid worms or Diptera larvae enclosed in fine-mesh litter bags significantly increased carbon mineralization through microbial respiration. In addition, Addison & Parkinson (1978) have shown that microbial respiration was enhanced in cores from tundra soils containing low numbers of mycophagous collembola compared with defaunated samples.

The dynamic effects of macroarthropod feeding activities on microbial respiration were investigated by Hanlon & Anderson (1980). Fragmented (2–4 mm) and mechanically ground (0.1–0.2 mm) oak leaf litter was inoculated with a mixed culture of fungi and bacteria and incubated in the laboratory. After 40 days both treatments showed similar levels of microbial respiration. Various numbers of woodlice (*Oniscus asellus* L.) or millipedes (*Glomeris marginata* Villers) were then added and respiratory rates were measured for a further 40 days.

Microbial respiration in fragmented litter was initially increased to twice the control rates by four *Oniscus* and to 1.6 times control rates by six *Glomeris* but subsequently declined to rates slightly above controls. However, cultures containing ten *Oniscus* showed respiratory rates below those of controls after 20 days. Cumulative carbon dioxide measurements, corrected for animal respiration, showed that microbial activity was decreased by grazing pressures higher than optimum values (Fig. 19.1). Animals feeding on previously ground litter produced a similar, reduced response suggesting that litter comminution was the main factor contributing to the enhancement of carbon mineralization but confirming that secondary effects were involved in the effects of the animals on microbial populations.
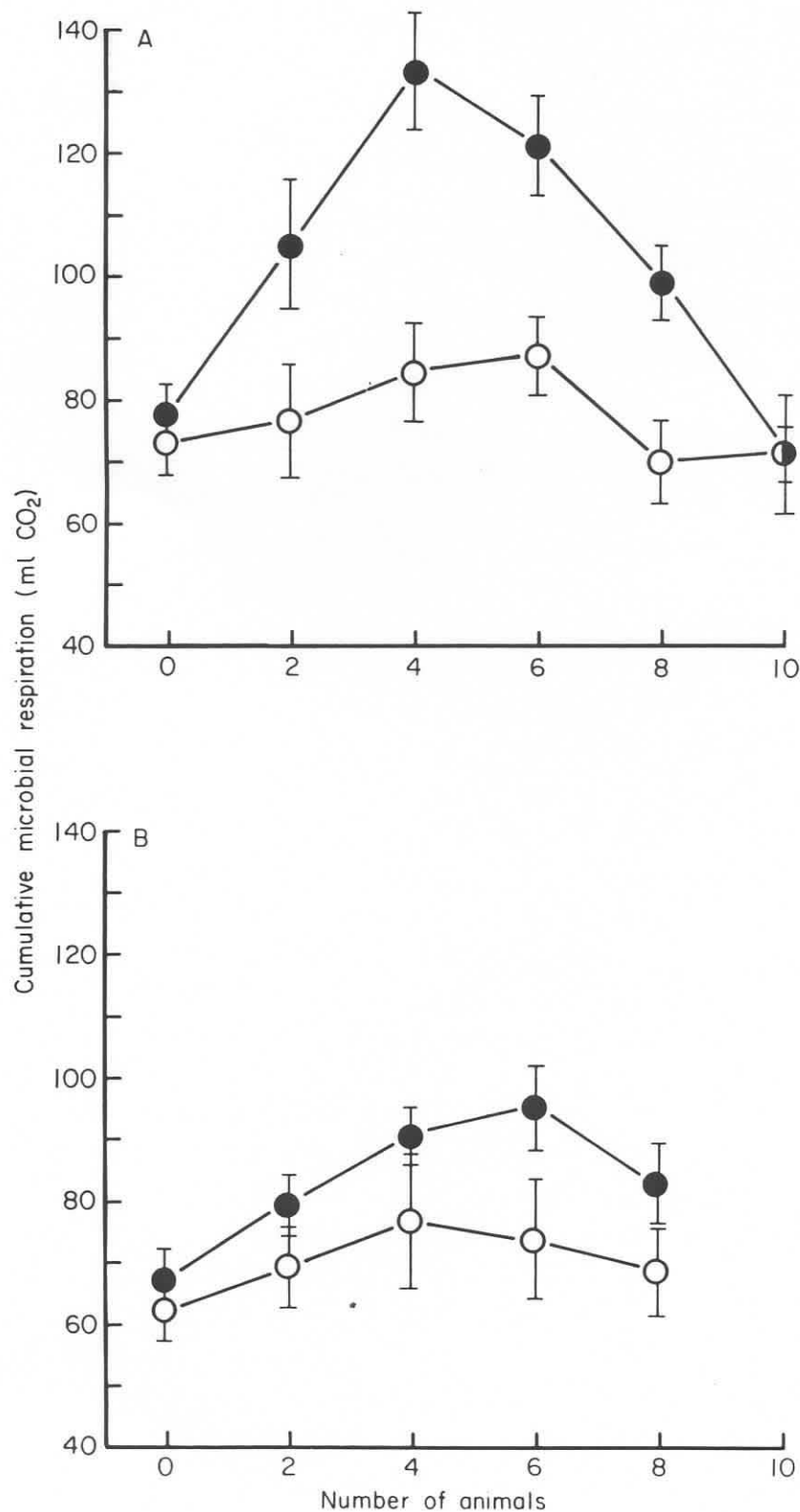
FIG. 19.1. Cumulative microbial respiration over 40 days (mean values $\pm$ 95% confidence limits) for different numbers of *Oniscus asellus* (A) and *Glomeris marginata* (B) feeding on 0.5 g oak leaf fragments ($\bullet$) or ground oak leaves ($\circ$). (After Hanlon & Anderson 1980.)

The effects of fungal grazing in the absence of litter comminution by the animals were investigated in experiments using mycophagous collembola (*Folsomia candida* Willem) to graze *Coriolus versicolor* (L.ex Fc) growing on ground leaf litter (Hanlon & Anderson 1979). Five collembola per 0.1 g leaf litter stimulated fungal respiration for approximately 14 days while higher numbers of animals, up to 20 individuals, produced no stimulatory effect or inhibited fungal respiration. All treatments were significantly below controls three weeks after the introduction of the animals. Total cumulative respiration showed a non-linear response to animal numbers similar to that shown in Fig. 19.1.

Hargrave (1970) has shown similar bell-shaped curves for the effects of amphipods on bacterial activity in lake sediments. In these experiments microbial activity was not inhibited until amphipod respiration (30 animals) accounted for 65% of community respiration. In the experiments reported here *Oniscus* produced an inhibitory response at only 13% of total respiration while the more selectively mycophagous collembola inhibited fungal activity at less than 5% of total respiration. These effects therefore fall within the animal densities and activity ranges found in natural soils.

While it can be concluded that optimum levels of soil animal feeding activities do enhance carbon mineralization rates by microorganisms, it is also evident that high feeding intensities can inhibit microbial activity. Investigation of this phenomenon has revealed gross changes in the balance of bacterial and fungal populations affected by animal feeding activities.

INTERACTIONS BETWEEN ANIMAL AND MICROBIAL POPULATIONS

Analysis of changes in bacterial and fungal populations in the above experiments (using direct count methods) revealed that reduced microbial respiration resulting from superoptimal levels of grazing by macroarthropods and collembola was associated with a reduction of fungal standing crop and an increase in bacteria (Hanlon & Anderson 1979, 1980). Results for *Oniscus* grazing fragmented litter are shown in Fig. 19.2. Fungal standing crop was reduced by all levels of animal feeding, the effects being particularly pronounced over the first three days of the experiment. After 35 days fungal standing crop was reduced by the animals to approximately one third of control levels. Bacterial standing crop, however, increased proportional to feeding intensity and after 35 days litter with six *Oniscus* contained ten times more bacteria than controls. Similar effects were detected in ground litter and in litter grazed by collembola and *Glomeris* (Table 19.1.)

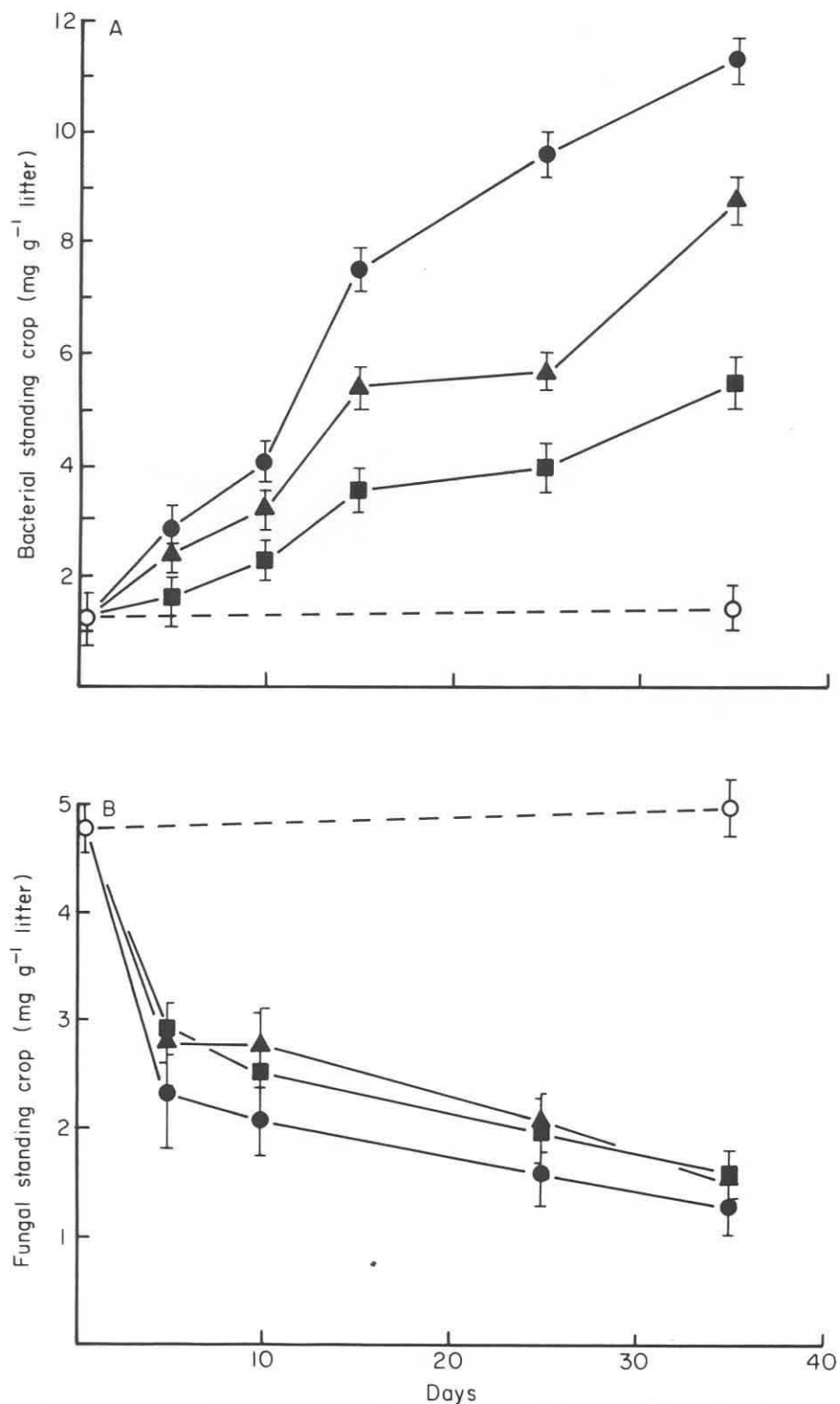Thus it is evident that not only slow-growing basidiomycetes such as

FIG. 19.2. Bacterial (A) and fungal (B) standing crops in 0.5 g fragmented oak leaf litter grazed by different numbers of *Oniscus asellus*. Mean values ($\pm$95% limits) are shown for control chambers without animals (O) and for chambers, containing 2 (■), 4 (▲) or 6 (●) animals. Microbial standing crops were determined by direct counts using membrane filters: 3 replicate chambers, 4 filters per replicate and 10 fields per filter ($n = 120$) for each estimate. Results are expressed as milligram of fungi or bacteria per gram dry weight litter. The small fiducial limits are typical of results using the filter technique. (After Hanlon & Anderson 1980.)

TABLE 19.1. Bacteria in the food, gut contents and faeces of *Glomeris marginata* and *Oniscus asellus*. Dilution series of litter, gut contents and faecal homogenates were prepared in 0.1% peptone water. Counts of viable bacteria were made using pour plates (Oxoid Nutrient Broth powder $13 \, \text{g} \, \text{l}^{-1}$; agar $15 \, \text{g} \, \text{l}^{-1}$). Nystatin ($50 \, \mu\text{g} \, \text{cm}^{-3}$) was included to suppress fungal growth. Homogenates of gut contents were filtered through weighed Millipore filters (0.45 μm pore size), dried in a vacuum oven for 48 hours and then reweighed to determine the dry weight of gut contents. Results are expressed as counts per gram dry weight material.

Sample	Replicate no.	Viable bacteria $(10^8 \, \text{g}^{-1})$	Mean $(10^8 \, \text{g}^{-1})$
Litter	1	3.4	
	2	6.7	4.3
	3	2.8	
Glomeris gut	1	13.0	
	2	11.9	22.8
	3	43.5	
Glomeris faeces	1	695.5	
	2	306.9	404.1
	3	209.9	
Oniscus gut	1	8.9	
	2	65.3	28.2
	3	10.3	
Oniscus faeces	1	437.5	
	2	386.0	349.6
	3	225.0	

C. versicolor but also the faster-growing microfungi, such as *Penicillium*, *Mucor* and *Trichoderma* which were dominant in the macroarthropod grazed litter, are extremely sensitive to animal feeding activities. The guts of macroarthropods are a favourable environment for bacterial growth (Reyes & Tiedje 1976; Anderson & Bignell 1980) and increased counts in gut contents and faeces of *Oniscus* and *Glomeris* are an evident consequence of gut passage (Table 19.2). These data simply refute the statement by Boyle & Michell (1979) that the guts of various crustacea, including *Oniscus asellus*, are sterile. Reyes & Tiedje (1976) observed that although the net effect of gut passage in *Tracheoniscus rathkei* Brandt (Isopoda) was an increase in bacteria over the food litter, lysis and digestion of bacterial cells also occurred. The same phenomenon has been established for *Glomeris* and 53.2%, 53.4%, and 28.9% of tritiated *Pseudomonas syringae*, *Erwinia herbicola* and *Escherichia coli* were assimilated (Anderson & Bignell, unpublished data).

The effects of animal grazing on microbial populations are further

TABLE 19.2. Effect of *Glomeris* numbers on bacteria populations in oak leaf litter from the experimental microcosms.
(a) Total viable counts using pour plates (see Table 19.1).
(b) Ammonifying bacteria estimated by the most probable number technique (MPN) using 0.2% tryptone medium (three series of five replicates). Results are expressed as counts per gram dry weight of litter.

| Treatment (no. animals) | (a) Total viable $(10^9\ g^{-1})$ | | | (b) Ammonifiers $(10^5\ g^{-1})$ | | |
	Replicate	Count	Mean	Series	Mean MPN	Overall mean MPN
0	1	2.6		1	0.04	
	2	1.9	1.87	2	0.01	0.04
	3	1.1		3	0.08	
4	1	2.4		1	0.7	
	2	0.9	2.17	2	0.3	2.47
	3	3.2		3	6.4	
8	1	12.0		1	4.0	
	2	2.0	6.00	2	4.0	4.00
	3	4.0		3	4.0	

complicated by the influence of resource quality on microbial populations and the quality of microbial tissues as a food resource for the animals. These interactions are further modified by the availability of microorganisms to the animals in soil and litter microhabitats.

Booth & Anderson (1979) demonstrated that the growth rates and reproduction of collembola (*Folsomia candida*) feeding on *Coriolus versicolor* were affected by the nitrogen content (as asparagine) of the fungal culture medium and hence the protein and amino acid content of the fungus. Egg laying rates at 200 μg l^{-1} N in the culture medium were over three times higher than at 2 μg l^{-1} N. A less marked reproductive response was found for another litter basidiomycete *Hypholoma fasiculare* Huds grown under the same conditions. These experiments have been repeated by Leonard (see p. 441, this volume) using *Mucor plumbeus* Bon. grown in two-dimensional and three-dimensional bead matrices at different nitrogen concentrations. The two-dimensional surface of fine glass beads exposes the fungus to attack by the collembola, and at 20 or 200 μg l^{-1}N the growth response of the animal population resulted in the elimination of the fungus. At 2 μg l^{-1} N an equilibrium was established because both the fungus and the collembola were nitrogen-limited but the fungus was apparently better adapted to these low nutrient conditions. In the three-dimensional matrix the effect of the higher

nitrogen levels was reversed. The beads formed a microhabitat refuge for the fungal hyphae, where they were protected against grazing, and the fungus proliferated under the same nutrient conditions where it had previously been reduced (Fig. 19.3). Experiments using more natural soil and litter systems are in progress but these results serve to illustrate that the feeding activities and
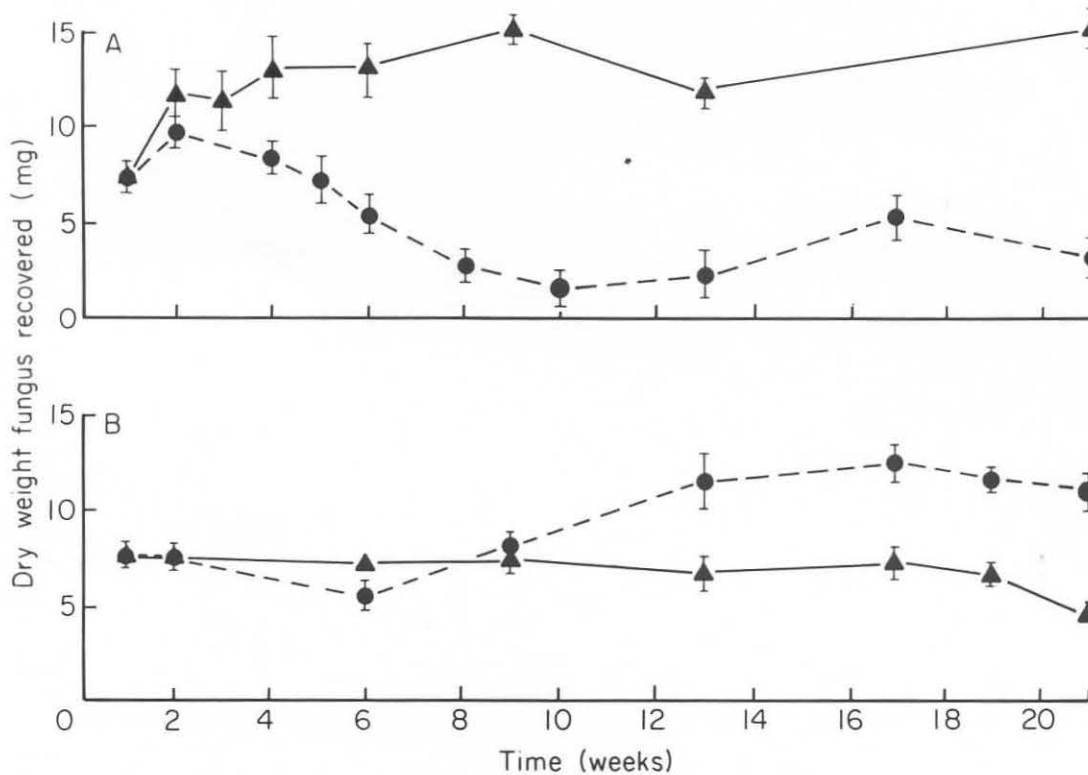

FIG. 19.3. Effect of spatial heterogeneity on the growth of *Mucor plumbeus* in controls (▲) and in cultures grazed by *Folsomia candida* (●). The fungus was grown in liquid medium containing 20 mg l^{-1} N (as asparagine) on a two-dimensional surface formed from fine glass chromatography beads (A) or in a three-dimensional matrix of ceramic column packing (B). The collembola were added seven days after the fungal inoculum. Fungal mycelium was recovered by washing and sonic separation from the matrix. Results are expressed as mean weight per culture ± 1 standard error ($n = 5$). (See also Leonard p. 441, this volume.)

effects of microarthropods on microbial populations are influenced by the structural complexity of soil and litter microhabitats as well as by the nutritional status of the litter for fungal growth.

Effects of animals on nutrient fluxes from decomposing leaf litter

The majority of studies emphasize the role of soil animals in carbon mineralization processes and flux rates of non-limiting, mineral elements including radio isotopes. There have been no detailed studies of animal–

microbial interactions in nitrogen flux pathways despite the recognized importance of nitrogen in limiting ecosystem processes and the large immobilized pools of organic nitrogen in most natural soils. Ausmus, Edwards & Witkamp (1976) have suggested that the soil fauna is critical for the mobilization of nitrogen in microbial tissues but there is no direct evidence for this phenomenon.

Current research in this laboratory is directed towards an understanding of the role of arthropods in nitrogen flux pathways in forest soils, particularly bacterially mediated steps in nitrogen transformations.

Investigations of these processes in the field are hindered by the biological and physico-chemical complexity of soils and their variability in time and space. At the other extreme, laboratory experiments may be difficult to extrapolate to field conditions because important synergistic effects may be excluded by an oversimplification of the system. Microcosms offer a means of bridging these extremes if a holistic approach is adapted to their design and analysis, while retaining the analytical precision of laboratory experiments and the ability to replicate them. The field system can be approached by either using microcosms of increasing complexity and evaluating the kinetics of compartments as they are added to the model, an approach developed by Patten & Witkamp (1967), or by using intact soil cores which are manipulated in the laboratory and their dynamics compared with field samples of lysimeters. The first generation of experiments reported here were not intended as analogues of natural systems but to form a link between the various phenomena described above and more complex systems.

Experiments were carried out to investigate the effects of macroarthropods on nutrient losses from decomposing oak (*Quercus robur* L.) leaf litter. Approximately 3 g of leaf litter fragments (2–4 mm) were placed in containers whose bases were covered with fine stainless steel mesh. The litter was inoculated with a homogenate of decomposing leaf litter and incubated for three weeks at 15°C before 0, 2, 4, 6 or 8 *Glomeris* or *Oniscus* were added. The containers were leached at intervals of seven days using distilled water and the leachates were analysed for calcium, potassium, sodium, ammonium, and nitrate.

Cation losses from leaf litter showed similar trends for treatments with *Glomeris* and *Oniscus* and are illustrated by the data for potassium shown in Fig. 19.4. Losses of potassium from controls followed an approximately negative exponential pattern. Treatments with *Glomeris* showed similar trends to the controls but cumulative release rates, although proportional to grazing intensity and generally significantly higher than controls ($P < 0.01$), showed only small increases in mineral nutrient mobilization in the presence of animals (see Fig. 19.5).
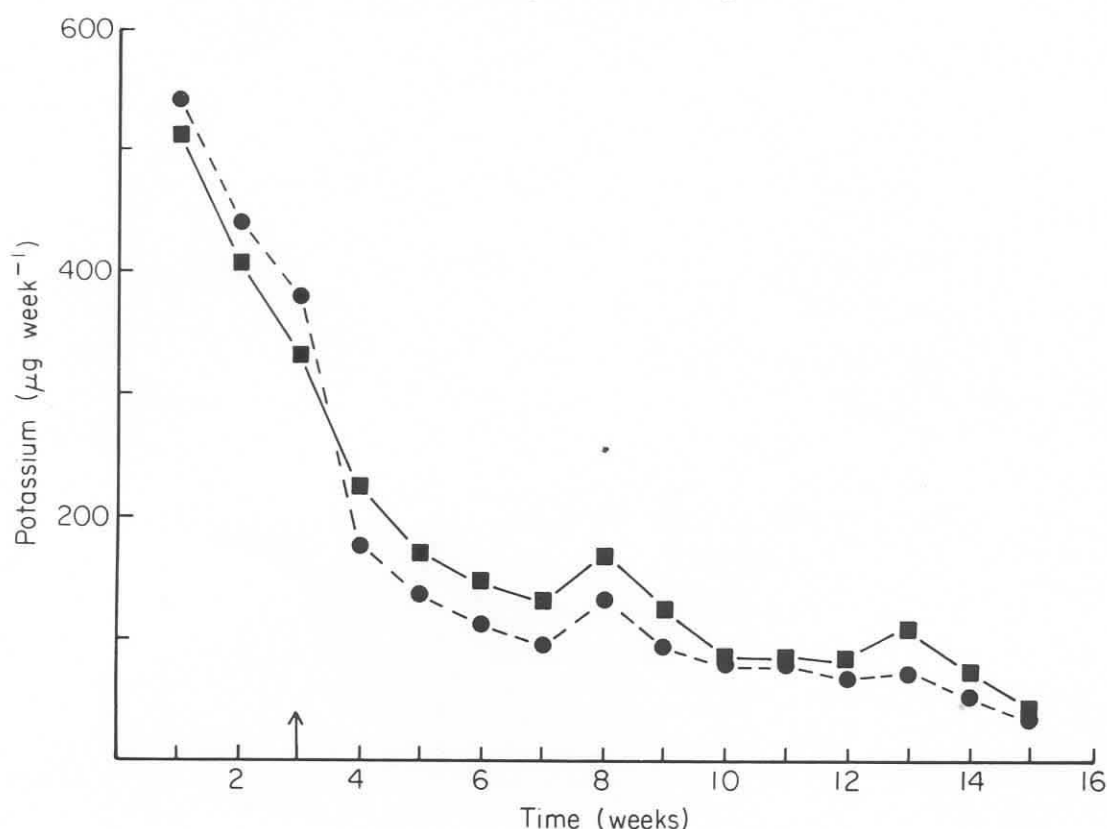
FIG. 19.4. The effect of *Glomeris* feeding activities on potassium fluxes from decomposing oak leaf litter. Aliquots of 3 g (dry wt.) fragmented leaf litter (3–5 mm) were added to microcosm chambers and leached in distilled water for 24 hours. The drained samples were inoculated with a litter suspension and incubated for three weeks at 15°C before 0, 2, 4, 6 or 8 animals were added (↑). Nine replicates of each treatment were prepared. The samples were leached with 60 ml distilled water every seven days and the mineral nutrient content of the leachates determined using an atomic absorption spectrophotometer (Pye Unicam SP9-800). Mean potassium concentrations in leachates are shown for chambers without animals (●) and for chambers containing 8 *Glomeris* (■). Results for treatments with 2, 4 or 6 animals were intermediate between these values and are not shown for clarity of presentation. Standard errors are obscured by the symbols in all cases.

Small losses of nitrate were detected in leachates from all treatments. This is in accordance with expectations that mineral nitrogen fluxes in acid litter would be predominantly in the form of ammonium.

The pattern of ammonium losses from controls showed a similar trend to cation leaching though initial loss rates were lower (Fig. 19.5). The effect of adding animals, however, was dramatically different to the pattern shown to the other nutrients. Ammonium losses from the litter were considerably enhanced by the presence of animals and after 16 weeks cumulative losses of ammonium were over three times higher than controls. Both instantaneous release rates and cumulative losses showed a non-linear response to the numbers of *Glomeris* reflecting the pattern shown for microbial respiration (see Fig. 19.1). Ammonium concentrations in leachates were increased by the
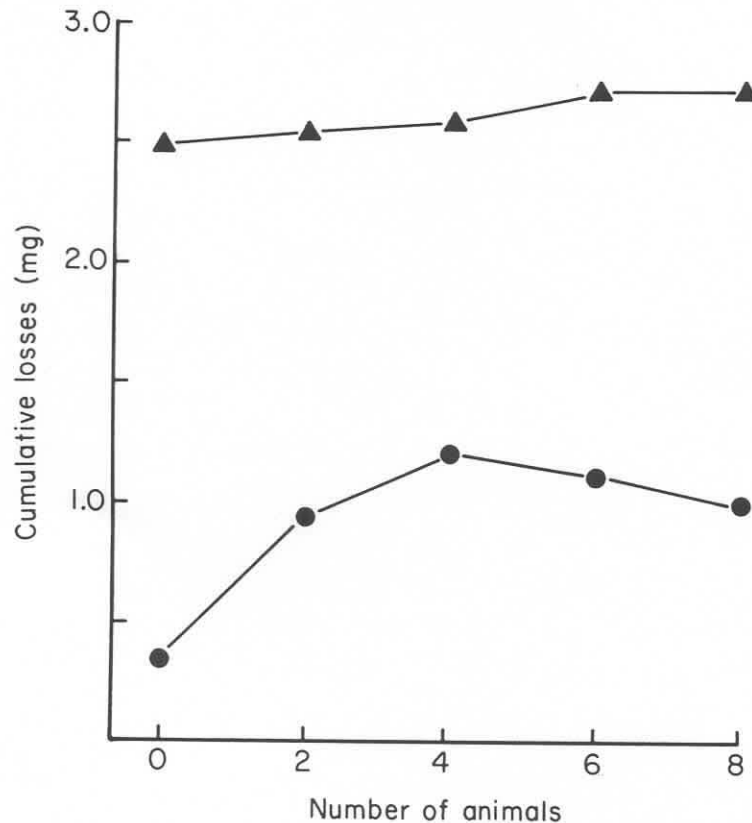
FIG. 19.5. Cumulative losses of potassium (▲) and ammonium (●) ions in leachates from chambers containing different numbers of *Glomeris* over 15 weeks.

addition of up to four animals but higher numbers reduced nitrogen losses as ammonium; ammonium concentrations in leachates from all treatments with animals were, however, considerably above those of the controls (Fig. 19.5). The removal of animals resulted in ammonium loss rates falling to approximately control levels over a period of 2–3 weeks (Fig. 19.6).

The addition of *Oniscus* to microcosms produced similar results to *Glomeris* in terms of cation and ammonium mobilization rates but, unlike the experiments with *Glomeris*, ammonium fluxes were proportional to the number of animals in the microcosms.

The mechanisms responsible for the different patterns of ammonium release by *Glomeris* and *Oniscus* have not yet been determined. They are not, however, simply related to the different nitrogenous excretory products of the two groups of animals. Most terrestrial arthropods, including millipedes, are generally assumed to excrete uric acid as an adaptation to water conservation (Chapman 1975). The principal nitrogenous excretory product of terrestrial isopods, however, is ammonia (Wieser & Schweizer 1970) reflecting their close physiological affinities to aquatic crustacea. It was initially hypothesized that the breakdown of uric acid in millipede faecal material might account for the continued release of ammonium from the litter for three weeks after the
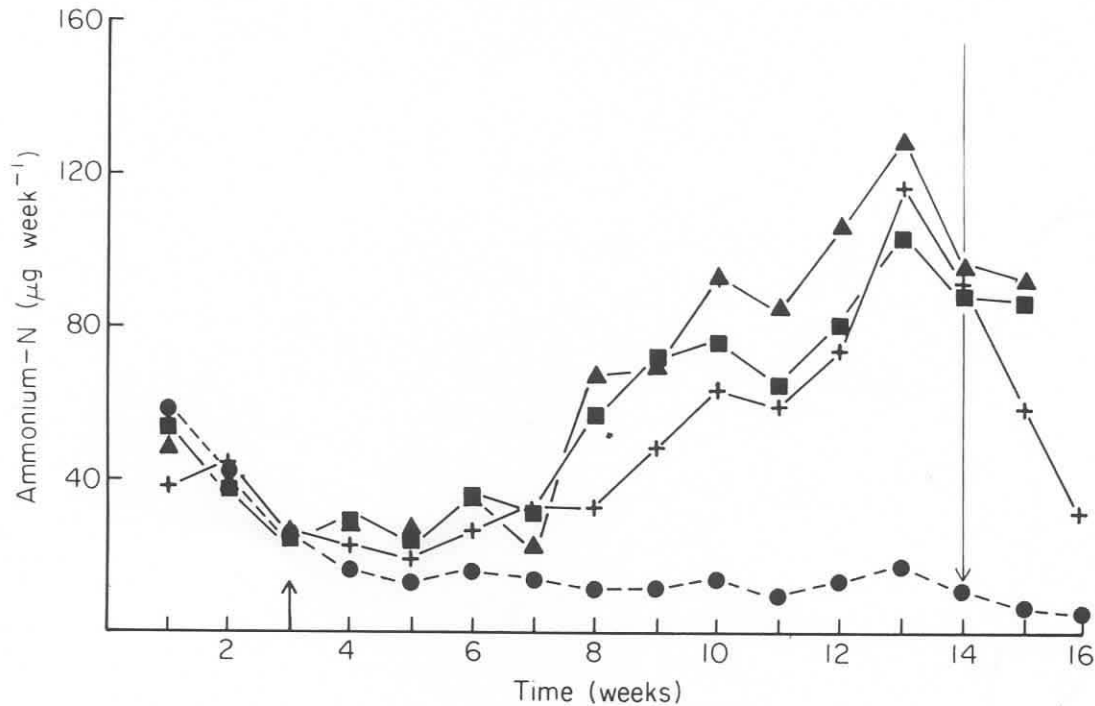
FIG. 19.6. Effect of *Glomeris* feeding activities on ammonium fluxes from decomposing oak leaves. Ammonium content of leachates was determined by Technicon Autoanalyser using the phenol method. Results are presented for mean ammonium losses from chambers containing 2 (+), 4 (▲) or 8 (■) *Glomeris* and for controls (●) without animals. Results for six animals were intermediate between those for four and eight animals and are not presented. Animals were removed from chambers containing two *Glomeris* at 14 weeks and ammonium concentrations in leachates, in the absence of feeding activities, were measured for a further two weeks. (See Fig. 19.4. for further details of methods.)

animals were removed. Faeces, gut contents, gut tissues and eviscerated bodies of *Glomeris* and *Oniscus* were assayed for uric acid. Homogenates were treated with pig liver uricase and measured spectrophotometrically at 292 nm (Uric Acid Diagnostic Kit No. 292-uv; Sigma Chemical Co., St Louis). No uric acid was detected in any of the preparations except for the body tissues of *Glomeris* which were found to contain up to 2.5% uric acid by weight. A similar phenomenon has been described by Mullins & Cochran (1976) who found that uric acid was absent from cockroach faeces but was sequestered in the fat bodies. These nitrogen reserves could be utilized by the animal as a response to low protein diets or oviposition. Potrikus & Breznak (1980a,b) have shown that uric acid can form up to 45% of the dry body weight of a wood-feeding termite and that the mobilization and re-utilization of the nitrogen is mediated by gut bacteria. Paradoxically, we have found uricolytic bacteria present at similar densities in the guts of *Glomeris* and *Oniscus*. Inorganic nitrogen available in the gut is in excess of that required by the proliferating bacterial flora and fresh faeces contain high concentrations of ammonium nitrogen (Table 19.3) as well as an increase in bacterial biomass through the gut passage (see Table 19.2).

TABLE 19.3. Changes in the nitrogen content of hazel litter eaten by *Glomeris* (from Bocock 1963).

Material	Amino-N $(\mu g\ g^{-1})$	NH_4^+ $(\mu g\ g^{-1})$	As % of total N	Total N $(\mu g\ g^{-1})$
Food	193	175	2.7	13 600
Uneaten food	86	335	3.2	13 100
Faecal pellets	103	1385	9.5	15 700

Experiments with these two macroarthropods reveal that cation leaching rates are not substantially increased through litter comminution but the animals appear to have a significant role in nitrogen mobilization and mineralization. This effect is not simply a function of the nitrogen excretion by the animals, since ammonium losses from the microcosms did not increase step-wise with the addition of animals, but involves qualitative and quantitative interactions with the litter microflora (see Table 19.2).

CONCLUSIONS

Soil animals may enhance or inhibit microbial activity, act differentially on bacterial and fungal populations, and directly or indirectly affect nutrient fluxes. These effects have primarily been demonstrated in litter systems but are not unrelated to field conditions since soil biological processes, including mycorrhizal activity, are mainly associated with the top 5 cm of organic soils. The influences of soil animals on microbial populations and nutrient fluxes may be related to major functional groups of the fauna and the structural characteristics of soil and litter habitats.

The microfauna (protozoa and nematodes) have small body sizes and short generation times which promote the regulation of bacterial populations through specific feeding activities and rapid population responses to changes in bacterial biomass. Bacterial populations in mineral soils are primarily energy-limited (Hisset & Gray 1976) and have mean generation times in the order of days rather than hours. In the rhizosphere, particularly in grasslands, microbial activity is promoted by root exudates, sloughed cells and the rapid turnover of root hairs. Competition for nutrients between the roots and rhizosphere microflora can occur under these conditions but Cole *et al.* (1978) have shown that the bacteriophagous microfauna can increase phosphorus turnover to rates comparable with aquatic systems.

The role of microfauna in acid, forest soils, where fungal biomass predominates, has not been quantified.

The mesofauna do not contribute significantly to the primary processes of litter comminution in forest soils and most collembola and mites are more cryptic than fossorial. The structure of soil and litter horizons therefore influences the availability of fungal hyphae as food resources (Anderson 1975). Fungal biomass increases during the early phases of litter decay if the leaves remain uncomminuted, but microarthropod gut contents generally contain decreasing amounts of hyphae after the winter months. This appears to be the result of fungi penetrating and ramifying the leaf tissues and thus reducing the amount of the mycelium exposed to attack on leaf surfaces. In addition, limiting nutrients are translocated to hyphal tips during growth and many of the hyphae bridging soil cavities åre highly vacuolated and a poor quality food resource for microarthropods. The high structural complexity of the surface layers of organic soils (Anderson 1978) modifies microarthropod population growth rates and their influences on nutrient mobilization through grazing effects.

The feeding activities of macrofauna modify these interactions through litter comminution, changing both the physical environment for fungal growth and the litter structural complexity, as well as altering the balance of fungal and bacterial populations. The selective destruction of the fungal component of the soil flora initially results in reduced soil microbial activity (Hanlon & Anderson 1980), followed by a 'flush of decomposition' as dead organisms are utilized by the proliferating bacteria. This flush can be measured in terms of carbon and nitrogen mineralization, and likened to the effects of fumigation (Jenkinson 1976). Macroarthropods significantly affect nitrogen mineralization rates through the combined effect of feeding, gut passage and excretion, and in the experiments reported here ammonium leaching was enhanced. Under natural conditions root and/or mycorrhizal uptake would form an ammonium sink and it was expected that in these experiments the high bacterial biomass in macroarthropod faeces would immobilize a major proportion of the available nitrogen. The observed ammonium concentrations in leachates implies, however, that bacterial growth is limited by resources other than nitrogen. This is in accordance with the view that the carbon and energy sources of structural polysaccharides in litter are unavailable to most bacteria but are attacked by many fungi (Eklund & Gyllenberg 1974). The feeding activities of the fauna may therefore temporarily shift the balance between mineralization and fungal immobilization so that mineral nitrogen is available to roots. Baath *et al.* (1978) have shown, using pot experiments, that the growth rate of pine seedlings was inhibited by treatments with glucose and nitrogen because nitrogen deficiency was induced by microbial growth and immobilization.

The importance of these nitrogen mineralization processes under field

conditions is unknown but it only requires the mobilization of a small proportion of the nitrogen pool in organic soils, which can be as high as 100 t ha^{-1} under mature conifers (Weetman & Webber 1972), to maintain the production of a climax woodland.

The role of grazing herbivores for nutrient cycles in grasslands is generally accepted by agriculturalists (Whitehead 1970; Floate 1970; Swift *et al.* 1979). It is reasonable to expect soil animals to have similar roles in decomposer systems where invertebrate biomass is usually one or two orders of magnitude higher per square metre than that of herbivores in the same ecosystem.

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REFERENCES

Addison J.A. & Parkinson D. (1978) Influence of collembolan feeding activities on soil metabolism at a high arctic site. *Oikos*, **30**, 529–38.

Aldag R. & Graff O. (1974) Einfluss der Regenwurm-tätigkeit auf Proteingehalt und Proteinqualität junger Haferpflanzen. *Zietschrift für Landwirt-schaftliche Forschung*, **31**, 277–84.

Anderson J.M. (1975) Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *Journal of Animal Ecology*, **44**, 475–96.

Anderson J.M. (1978) Inter- and intra-habitat relationships between woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia*, **32**, 341–8.

Anderson J.M. & Bignell D.E. (1980) Bacteria in the food, gut contents and faeces of the litter feeding millipede *Glomeris marginata* (Villers). *Soil Biology and Biochemistry*, **12**, 251–4.

Ausmus B.S., Edwards N.T. & Witkamp M. (1976) Microbial immobilisation of carbon, nitrogen, phosphorus and potassium: implications for forest processes. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (eds J. M. Anderson & A. Macfadyen), pp. 397–416. Blackwell Scientific Publications, Oxford.

Bååth E., Lohm U., Lundgren B., Rosswall T., Söderström B., Sohlenius B. & Wirén A. (1978) The effect of nitrogen and carbon supply on the development of soil organism populations and pine seedlings: a microcosm experiment. *Oikos*, **31**, 153–63.

Barsdate R.J., Fenchel T. & Prentki R.T. (1974) Phosphorus cycle of model ecosystems: significance for decomposer food chains and effects of bacterial grazers. *Oikos*, **25**, 239–51.

Bocock K.L. (1963) The digestion of food by *Glomeris*. In *Soil Organisms* (eds J. Doeksen & J. van der Drift), pp. 85–91. Elsevier-North Holland, Amsterdam.

Booth R.G. & Anderson J.M. (1979) The influence of fungal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). *Oecologia*, **38**, 317–23.

Boyle P.J. & Mitchell R. (1979) Absence of micro-organisms in Crustacean digestive tracts. *Science*, **200**, 1157–9.

Chapman R.F. (1975) *The Insects: Structure and Function*. English Universities Press, London.

Cole C.V., Elliot E.T., Hunt H.W. & Coleman D.C. (1978) Trophic interactions in soils as they affect energy and nutrient dynamics. V. Phosphorus transformations. *Microbial Ecology*, **4**, 381–7.

Cooper D.C. (1973) Enhancement of net primary productivity of herbivore grazing in aquatic laboratory microcosms. *Limnology and Oceanography*, **18**, 31–7.

Edwards C.A. & Lofty J.R. (1978) The influence of arthropods and earthworms upon root growth of direct drilled cereals. *Journal of Applied Ecology*, **15**, 789–95.

Eklund E. & Gyllenberg H.G. (1974) Bacteria. In *The Biology of Plant Litter Decomposition* (eds C. H. Dickinson & G. J. F. Pugh), pp. 245–68. Academic Press, London & New York.

Fenchel T. & Harrison P.G. (1976) The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (eds J. M. Anderson & A. Macfadyen), pp. 285–99. Blackwell Scientific Publications, Oxford.

Flint R.W. & Goldman C.R. (1975) The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. *Limnology and Oceanography*, **20**, 935–44.

Floate M.J.S. (1970) Mineralisation of nitrogen and phosphorus from organic materials of plant and animal origin and its significance in the nutrient cycle of grazed upland and hill soils. *Journal of the British Grassland Society*, **25**, 295–302.

Gosz J.R., Likens G.E. & Bormann F.H. (1973) Nutrient release from decomposing leaf and branch litter in Hubbard Brook Forest, New Hampshire. *Ecological Monographs*, **47**, 173–91.

Graff O. (1970) Phosphorus content of earthworm casts. *Landbau Forschung Völkenrode*, **20**, 33–6.

Hanlon R.D.G. & Anderson J.M. (1979) The effects of collembola grazing on microbial activity in decomposing leaf litter. *Oecologia*, **38**, 93–9.

Hanlon R.D.G. & Anderson J.M. (1980) The influence of macroarthropod feeding activities on microflora in decomposing oak leaves. *Soil Biology and Biochemistry*, **12**, 255–61.

Hargrave B.T. (1970) The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. *Limnology and Oceanography*, **15**, 21–30.

Hissett R. & Gray T.R.G. (1976) Microsites and time changes in soil microbe ecology. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (eds J. M. Anderson & A. Macfadyen), pp. 23–39. Blackwell Scientific Publications, Oxford.

Jenkinson D.S. (1976) The effects of biocidal treatments on metabolism in soil. IV. The decomposition of fumigated organisms in soil. *Soil Biology and Biochemistry*, **8**, 203–8.

McBrayer J.F., Reichle D.E. & Witkamp M. (1973) *Energy flow and nutrient cycling in a cryptozoan food web*. Oak Ridge National Laboratory. EDFB-IBP-73-8.

McDiffett W.F. & Jordan T.E. (1978) The effects of an aquatic detritivore on the release of inorganic N and P from decomposing leaf litter. *American Midland Naturalist*, **99**, 36–44.

Mitchell R. & Alexander M. (1963) Lysis of soil fungi. *Canadian Journal of Microbiology*, **9**, 169–77.

Mullins D.E. & Cochran D.G. (1976) A comparative study of nitrogen excretion in twenty-three cockroach species. *Comparative Biochemistry and Physiology*, **53A**, 393–9.

Nicholson P.B., Bocock K.L. & Heal O.W.H. (1966) Studies on the decomposition of the faecal pellets of a millipede (*Glomeris marginata* Villers). *Journal of Ecology*, **54**, 755–66.

Nixon S.W., Oviatt C.A. & Hale S.S. (1976) Nitrogen regeneration and the metabolism of coastal marine bottom communities. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (eds J.M. Anderson & A. Macfadyen), pp. 269–83. Blackwell Scientific Publications, Oxford.

Parle J.N. (1963) A microbiological study of earthworm casts. *Journal of General Microbiology*, **31**, 13–22.

Patten B.C. & Witkamp M. (1967) System analysis of [134]Cesium kinetics in terrestrial microcosms. *Ecology*, **48**, 814–24.

Potrikus C.J. & Breznak J.A. (1980a) Uric acid in wood eating termites. *Insect Biochemistry*, **10**, 19–27.

Potrikus C.J. & Breznak J.A. (1980b) Uric acid degrading bacteria in guts of termites. *Applied and Environmental Microbiology*, **40**, 117–24.

Reyes V.G. & Tiedje J.M. (1976) Ecology of the gut microbiota of *Tracheoniscus rathkei* (Crustacea, Isopoda). *Pedobiologia*, **16**, 67–74.

Sharpley A.N., Syers J.K. & Springett J.A. (1979) Effect of surface-casting earthworms on the transport of phosphorus and nitrogen in surface run-off from pasture. *Soil Biology and Biochemistry*, **11**, 459–62.

Sheilds J.A., Paul E.A., Lowe W.E. & Parkinson D. (1973) Turnover of microbial tissue in soil under field conditions. *Soil Biology and Biochemistry*, **5**, 753–64.

Standen V. (1978) The influence of soil fauna on decomposition by microorganisms in blanket bog litter. *Journal of Animal Ecology*, **47**, 25–38.

Swift M.J. (1973) The estimation of mycelial biomass by determination of the hexosamine content of wood tissue decayed by fungi. *Soil Biology and Biochemistry*, **5**, 321–32.

Swift M.J., Heal O.W. & Anderson J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford.

Syers J.K., Sharpley A.N. & Keeney D.R. (1979) Cycling of nitrogen by surface casting earthworms in a pasture ecosystem. *Soil Biology and Biochemistry*, **11**, 181–5.

Van der Drift J. & Witkamp M. (1960) The significance of the breakdown of oak litter by *Eniocyla pusilla* Burm. *Archives Néerlandaises de Zoologie*, **13**, 486–92.

Weetman G.F. & Webber B. (1972) The influence of wood harvesting on the nutrient status of two spruce stands. *Canadian Journal of Forest Research*, **2**, 351–69.

Whitehead D.C. (1970) *The role of nitrogen in grassland productivity*. Bulletin 48, Commonwealth Agricultural Bureau, Farnham Royal, Bucks.

Wieser W. & Schweizer, G. (1970) A re-examination of the excretion of nitrogen by terrestrial isopods. *Journal of Experimental Biology*, **52**, 267–74.

Witkamp M. (1969) Environmental effects on microbial turnover of some mineral elements. Part I – Abiotic factors. *Soil Biology and Biochemistry*, **1**, 167–76.

Witkamp M. & Barzansky B. (1968) Microbial immobilisation of ^{137}Cs in forest litter. *Oikos*, **19**, 392–5.

Witkamp M. & Frank M.L. (1969) Cesium-137 kinetics in terrestrial microcosms. In *Proceedings of the Second National Symposium on Radioecology* (eds D. J. Nelson & F. C. Evans), pp. 635–43. US AEC Conference–670503, US Department of Commerce, Springfield, Virginia 22151.

Witkamp M. & Frank M.L. (1970) Effects of temperature, rainfall and fauna on transfer of ^{137}Cs, K, Mg and mass in consumer-decomposer microcosms. *Ecology*, **51**, 465–74.

Wood T.G. & Sands W.A. (1977) The role of termites in ecosystems. In *Production Ecology of Ants and Termites* (ed. M. V. Brian), pp. 245–92. Cambridge University Press, Cambridge.